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Interhemispheric Communication Through the Corpus Callosum

Mnemonic Carry-Over Between the Hemispheres

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The early brain anatomists assumed highly important functions for the corpus callosum in relating and coordinating the activities of the two cerebral hemispheres. Likewise, the early clinical neurologists believed that destruction of this largest of all fiber tracts in the brain would result in serious functional defects, even in a general intellectual deterioration. However, actual observations on the effect of complete surgical section or of total agenesis of the corpus callosum in man and other animals have indicated a surprising absence of deficit.[1-6,8,9] This wide discrepancy between the expected and the actual effects of callosal damage has remained one of the enigmas of brain function.

Recent investigations of contralateral transfer of training in callosum-intact and callosum-sectioned animals, however, begin to reveal a definite role for the corpus callosum in the realm of "psychic" function. In the cat with the crossed retinal fibers divided at the optic chiasm, visual discriminations learned with one eye are recalled readily with the other eye, whereas such recall fails entirely when callosum also was sectioned prior to training.[12,13,16] Similarly, in the normal cat, discriminative learning with one forepaw is distinctly aided by prior identical learning with the other forepaw, whereas this cross benefit fails in the callosum-sectioned cat.[17] Thus, in the cat, one hemisphere seems in some way to benefit from the prior training or experience of the other hemisphere through intercommunication via the corpus callosum.

The present paper is an attempt to investigate further the nature of the callosal contribution. Does one hemisphere establish lasting memories of its own training or experiences in the other hemisphere, or does it merely make available to the other hemisphere mnemonic-loaded information for its sampling or use, without permanent contralateral trace establishment?

The general plan involved the destruction of crossed retinal fibers at the optic chiasm and subsequent establishment of pattern discrimination learned through one eye. The visual cortex plus varying amounts of adjoining cortex were then removed from the hemisphere receiving impulses from the trained eye. Survival of the learned responses was thereafter tested through the untrained eye. Preservation of the learned discrimination under these conditions would indicate the establishment of a duplicate memory system in the contralateral hemisphere.

Methods

Animals.—Fourteen cats were used, all of them laboratory-reared from an age of 6 weeks or younger. At the start of the present experiment they ranged in age from 7 to 14 months and had had no prior experience with formal visual training.

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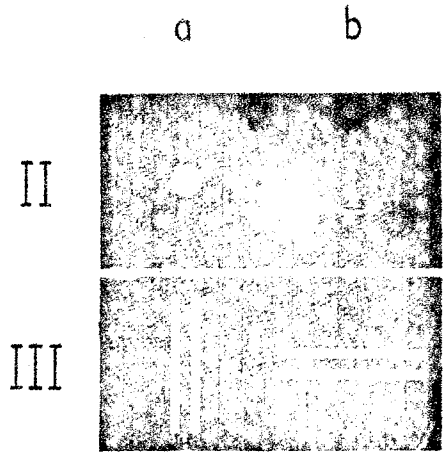

Fig. 1.—The two pairs of visual discrimination patterns. The left one of each pair was the positive (rewarded) pattern. The designations correspond to those in a preceding study.[10]

Surgical Procedures.—Section of the crossed optic fibers at the chiasm was effected through a transbuccal approach, as previously described.[10] The cortical ablations, carried out after establishment of the learned responses, were performed with routine neurosurgical techniques, the brain tissue being removed by suction. The extent of the cortical removals is described below.

Training and Testing Procedures.—The mask used during the periods of training and testing to occlude one or the other eye was constructed of soft black rubber sheeting and was held snugly in place by ties to a leather collar.

Two different discrimination problems were used. The paired test patterns for these are pictured in Figure 1. Discrimination on the basis of total luminous flux, rather than pattern, was ruled out in this study by designing the positive and negative patterns of equal area. Further, tests run with an imposed brightness difference between the patterns, with the more brightly transilluminated figure varying between the positive and the negative pattern, did not disrupt the response. The same training box and procedures were used as described earlier.[12] In establishing a discrimination, the two patterns of a pair were presented side by side, and the cats were trained to choose one of the two. The two patterns were switched from side to side according to a chance sequence to avoid development of side preference. After the cats attained correct performance of 34 or more trials out of 40, the responses were further stabilized by 400 overtraining trials, run in sessions of 40 per day.

Postoperative tests with the mask covering the trained eye were started on the 12th day following the cortical ablation, and, where immediate recall was not apparent, were continued in most cases until high-level performances were obtained.

Anatomical Controls.—When the behavioral testings were completed, the cats were given a lethal dose of pentobarbital and perfused with 10% formalin. The brains were removed, and completeness of chiasm section was confirmed by gross dissection and removal of the tantalum foil insert (Myers[12]). Determinations of extent of the cortical removals based on careful study of the gross brain specimens and gross brain sections proved adequate for the purposes of the experiment.

Three types of cortical removals were performed, as illustrated in Figure 2. The *minimal*-type lesion, as seen in Case *Msy*, was restricted to removal of an area approximately coextensive with the primary visual area as mapped by Talbot and Marshall.[18] The *moderate*-type lesion involved removal of this area plus adjoining, physiologically related cortex, as shown in *Chr*. Both types of lesions extended medially and ventrally to include the superior bank of the sulcus splenialis, leaving gyrus splenialis intact. The *maximal*-type lesion

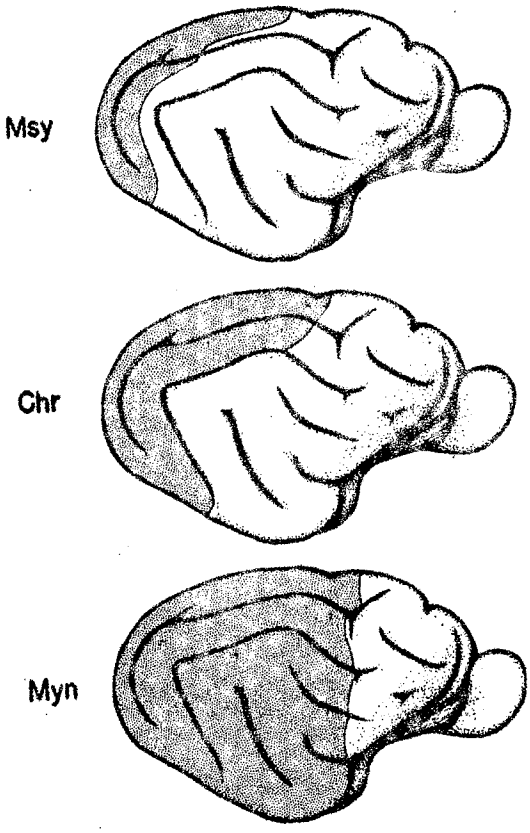

Fig. 2.—Stylized diagrams illustrating extent of cortical removal in the three lesion types. Variations in extent of lesion within a group were minor.

TABLE 1.—*Performance with Untrained Eye on Discrimination III After Destruction of Contralateral "Trained" Cortex*

Cat	Eye Tested	Lesion Type	Test Performance on Successive Days as Number Correct in Sets of 40		
			1st	2d	3d
Msy	L	R; minimal	37	--	--
Msf	L	R; minimal	37	--	--
Grs	L	R; minimal	26	36	40
Fst	R	L; moderate	30	38	38
Pln	R	L; moderate	27	40	--
Crw	R	L; moderate	28	32	38
Spc	L	R; moderate	33	38	--
Osw	L	R; moderate	40	--	--
Sch	L	R; moderate	37	--	--
Chr	L	R; moderate	39	--	--
Nkm	R	L; extensive	7/10 *	--	--
Kmn	R	L; extensive	37	--	--
Myn	L	R; extensive	27	37	40

* Nkm refused to run after 10 test trials, having erred in the last 3.

represented removal of all neocortex posteriorly with complete preservation of cortex anterior to and including the posterior sigmoid and coronal gyri (Case *Myn*). Variations in the extent of removal within these three groups were so slight as not to merit separate consideration. Removals in all cases extended through the entire depth of the gray matter and into the immediately subjacent white matter. The deep-lying ganglionic masses, including amygdala, were not encroached upon by the lesion and, as may be seen from Figure 1, *Myn*, the piriform cortex was preserved without damage.

Behaviorally, no bizarre effects were noted and no apparent alteration found in emotional behavior. There was demonstrable, however, the expected loss of visual responsiveness in the eye ipsilateral to the lesion, as tested by confrontation. In the cats with extensive lesions, transitory postural abnormalities were noted in the extremities contralateral to the lesion, which cleared within 5-10 days.

Results

The results obtained in the use of the two discriminations are described separately and are separately summarized in Tables 1 and 2.

Discrimination III.—Minimal-Type Lesion: Of three cats with the minimal-type lesion, two performed well from the beginning of testing with the untrained eye on Discrimination III. Each of these two cats made only 3 mistakes on the first 40 trials, and these were widely distributed through the trials. The third cat showed an apparently chance performance on the first set of 40 runs but achieved a high-level performance on the second and a perfect performance on the third set of 40 trials.

Moderate-Type Lesion: Among the seven cats with the moderate-type lesion three showed high-level performance on the first set of 40 trials; three, high-level performance on the second set of 40 trials, and the remaining cat, high-level performance only on the third set of 40 trials. In the case of all cats with the moderate-type lesion the performance level was well above chance on the first 40 trials.

Maximal-Type Lesion: Of the three cats with the maximal-type cortical removal, two showed good retention on the first trials, though one of the two, Nkw, a very anxious cat, refused to continue further trials after having run the first 7 of 10 correctly. The third cat, with extensive removal, after having shown significant retention on the first 40 trials, achieved high-level performance on his second 40 trials.

The two types of results obtained with the cats on Discrimination III are illustrated in Figure 3. The curves of *Chr* demonstrate the usual slow learning rate during initial training and the almost perfect recall on test trials with the untrained eye. The curves of *Myn* indicate only partial recall, with, however, clear-cut saving in relearning with the untrained eye.

Discrimination II.—Discrimination II is the more difficult discrimination of the two,

TABLE 2.—*Performance with Untrained Eye on Discrimination II After Destruction of Contralateral "Trained" Cortex*

Cat	Eye Tested	Lesion Type	Test Performance on Successive Days as Number Correct in Sets of 40			
			1st	2d	3d	4th
Chr	L	R; moderate	25	25	25	32
Myn	L	R; extensive	18	21	21	25
Bhf	L	R; extensive	23	--	--	--

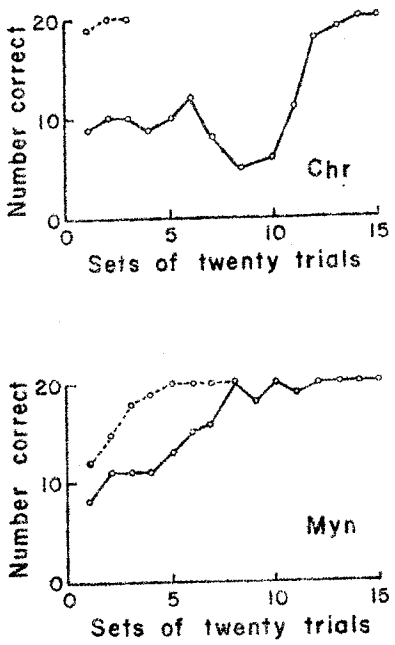

Fig. 3.—Performance of *Chr* and *Myn* on Discrimination III. The solid line represents initial training with one eye, while the dashed line indicates the performance on test trials using the second, untrained eye. *Chr* illustrates immediate recognition with the untrained eye, while *Myn* shows considerable saving in relearning with the untrained eye.

as gauged by the far greater number of trials required for initial learning and by the general behavioral response of the cats during training. Only three cats were tested on this discrimination—one having the moderate and two the extensive lesion. The cat with the moderate-type cortical lesion showed little, if any, immediate retention and only suggestive evidence of saving in relearning of this response with the untrained eye, as demonstrated best in the graph of Figure 4 (*Chr*). Cat *Myn*, with the extensive lesion, showed also no immediate retention and little indication of saving on relearning with the untrained eye (*Myn*, Fig. 4). Cat *Knt* was tested only for 40 trials and showed no apparent retention.

Comment

Destruction bilaterally of the primary visual cortical areas in the cat results in loss of pattern discriminations of the sort used in the present experiment. In like manner, transection of the great cortical commissure, the corpus callosum, completely prevents visual gnostic intercommunication between the brain halves in the cat (see Introduction). These facts point to cortex (and associated thalamic nuclei) as the probable site of elaboration of visual sensory input. The contribution of brain-stem mechanisms to such high-level, "phychic" activity has yet to be fully explored. Present evidence, however, points toward involvement of brain stem in preparing and maintaining levels of activity in the cortex necessary for such high-level functions, rather than toward a primary involvement in these functions.[7,11] Accordingly, it is assumed in the following discussion that the memory mechanisms underlying the involved pattern discrimination responses re-

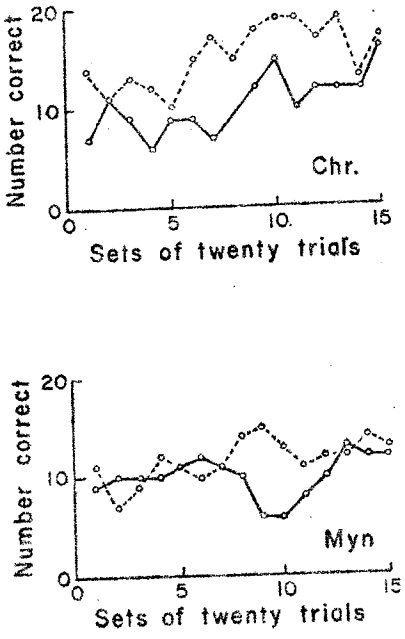

Fig. 4.—Performance of *Chr* and *Myn* with Discrimination II on initial training, using one eye (solid line), and on retraining, using the opposite, untrained eye (dashed line). Training and testing procedures with this response were not strictly comparable, owing to need for variable encouragement. Therefore only the first 300 trials with each eye are represented. Neither cat shows definite indication of immediate recognition with the untrained eye. On the contrary, only slight saving is suggested on retraining in the case of *Chr* and no saving in the case of *Myn*.

side somewhere within the cortical gray mantle, or at least can be grossly disorganized by appropriate cortical insult.

Widespread destruction of the cortex of the "trained" hemisphere does not destroy recall of the simpler Discrimination III by the opposite "untrained" hemisphere, though some uncertainty is seen on test performance in a few instances. On the other hand, there is complete or near-complete loss of memory for the more difficult Discrimination II, and it is necessary to reteach this response to the untrained eye. A closely similar outcome, with good preservation of the simpler and loss of the more difficult discrimination, has been seen on tests with the "untrained" hemisphere of chiasm-sectioned cats having transection of the corpus callosum subsequent to training but prior to testing.[15] However, section of the corpus callosum in this latter study did not noticeably affect levels of performance with the "trained" hemisphere, though this was often the hemisphere receiving retraction during entry for callosum section. Such close dependence of the results on training history and lack of relation to fortuitous surgical manipulation render unlikely the suggestion that gnostic losses of the "untrained" hemisphere are due to "threshold diaschisis" effects secondary to the surgical procedures.

One hemisphere seems, therefore, to have the capacity to establish well-marked and lasting memory traces in the opposite hemisphere through the corpus callosum if the communication handled is of simpler dimensions. With more difficult transmissions, however, there is apparent lack of contralateral engram establishment, with loss of recall capacity contralaterally on section of the corpus callosum or destruction of ipsilateral "trained" cortex. It must be noted at this time that cats with chiasm section alone, without the superimposed callosal or cortical lesions, have no difficulty in recalling the more difficult Discrimination II on transfer tests with the untrained eye. It may be inferred from this that the cortex removed from the "trained" hemisphere normally must contribute actively and substantially to performance with the "untrained" hemisphere at the time of responding.

Two activities may then be distinguished for the corpus callosum in visual gnostic interconmunication. The one, limited somewhat in its capacity, may result in establishment of a lasting contralateral memory trace somewhat less well developed than on the trained side. This activity is accomplished at a time prior to testing. The second activity, though not effective in further trace establishment, contributes potently to discriminative response and is achieved at the time of testing. The relationship between these two contributions is not known. It seems most likely that they are aspects of one and the same mechanism, which may affect neuronal events of the opposite hemisphere in lasting, as well as nonlasting, supportive ways. Fuller understanding of these results in terms of neuronal events, however, awaits further investigation.

No gross differences were seen among the cortical lesion types in their effects on performance level with the opposite, "untrained" neural apparatus, as seen from Tables 1 and 2. Differences in performances were far greater within than between lesion types, and greater deficits were not necessarily seen with greater lesions. This approximate equivalence of the lesion types would support the concept that neural tissue beyond the more restrictive removal contributes little toward the maintenance, and presumably also the development, of stable contralateral memory effects. The cortex in and around the visual receptive areas would then appear not only to receive the visual impulses from the retina but also to integrate and subsequently to intercommunicate between the hemispheres the significance of this experience. Data indicating a posterior localization of the visual gnostic transfer function of the corpus callosum tends to lend further support to this

interpretation, in view of the primarily homologous nature of the callosum interconnections.[14]

Summary

Fourteen chiasm-sectioned cats were taught visual pattern discriminations with one eye masked. Thereafter the primary visual area, plus varying amounts of adjoining cortex, was removed from the hemisphere of the trained side. Beginning 12 days after the cortical removal, the cats were tested for their ability to recall the response with the untrained eye. Recall was immediate, or nearly so, for the simpler discrimination. Recall failed, however, in the case of the more difficult discrimination. Amount of cortical tissue removed beyond the receptive area did not appear to affect this outcome.

The results demonstrate that the hemispheric intercommunication through the corpus callosum is sufficiently developed to establish independent memory traces in the opposite hemisphere when the involved integration is of simpler dimensions, but may fail when the problem is more complex. It is shown also how one hemisphere may actively contribute to the performance of the other at the time of response through the corpus callosum.

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